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Neural Mechanisms in Visual Guidance of Limb Movement

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Limb movements may be coordinated and executed entirely in the absence of vision. Normally, however, visual impressions play an important role in directing motor response. Sometimes visual direction appears merely as a superimposition upon already established patterns of activity. In progression, obstacles or irregularities seen in the path may condition final placement of the limbs. At other times visual direction appears to enter more intimately to define the particulars of movements from their inception. Reaching out to grasp a glass of water or to seize a fleeting object requires a close correlation of vision with patterning of action.

Little is known of the neural organizations through which visual information may impinge upon motor mechanisms. In the absence of definite knowledge brain schemata have been proposed to suggest possible pathways and centers through which visuomotor coordination might occur. Most schemata have implied a transmission of visual information from the visual receptive area in the occipital lobe to central motor cortex either

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directly or following synaptic interruption in intervening cortical regions. Such a schema was outlined by Bechterev [2] who suggested that visual impulses may pass from calcarine cortex through the receptive manual area in the postcentral gyrus to allow for a direct visual control of hand movements. In addition, he put forward that impulses also may pass to the area of concentration in the prefrontal cortex from which they can be relayed to the appropriate manual motor area in precentral gyrus for that direction of manual movements issuing from "inner stimulation." More recent formulations have, in general, resembled Bechterev's early schema (see, for example, Walshe,[10] von Bonin,[9] and others). Tower [8] has referred to the precentral convolution as a sort of keyboard upon which impulses from other cortical areas may play to gain motor expression.

Propositions out of accord with the general concept of flow of impulses from sensory areas through precentral motor convolution have been set forth. Lashley [4] has spoken against direct precentral cortical participation in skilled acts. Instead, he put forward the idea that precentral motor centers may contribute to response only "as a part of the kinetic mechanisms for reflex control of spinal posture and for maintenance of excitability of lower motor centers."

Penfield [7] has advocated still another concept of visuomotor coordination based on stimulations and ablations carried out during therapeutic neurosurgical interventions on humans. Patterns of visual stimuli destined to regulate motor response, he believes, are channeled first inwards from occipital cortex to a central integrating mechanism, subsequently to be redirected outwards to precentral cortex where the final pattern of volitional activity is elicited. Transgriseal and white matter associational conduction between occipital lobe and central cortex are deemed unnecessary for visual direction of limb response.

The present study seeks to put to test these various brain schemata by determining the importance of several different neural pathways for the visual control of forelimb movement. In a first part, the contribution of direct corticocortical linkages between occipital cortex and the cortex of the pre- and postcentral gyrus was investigated in cats and monkeys with disruptive transverse wedge resections between the occipitotemporal and the frontoparietal lobes of the 2 hemispheres. In a second part, the importance of the forebrain commissures to crossed eye-hand coordination was examined in animals after removal of the occipital lobe of one hemisphere and the pre- and postcentral regions of the other hemisphere in combination with division of corpus callosum, anterior commissure, and, in some instances, the massa intermedia. Deficiencies in eye-hand coordination were assessed by comparing preoperative and postoperative performances in a series of tests of visuomotor skills.

Methods

Animals.—Seven adult cats and 5 immature rhesus monkeys served as subjects. The animals were known to the experimenters prior to the study and were chosen because of their docility and ease of handling. They were repeatedly subjected both before and after the cerebral lesions to the same battery of behavioral test procedures.

Surgical Procedures.—Similar surgical procedures were used for both the cats and the monkeys. Under pentobarbital anesthesia, a large unilateral bone-flap was removed and placed in isotonic saline. The dura was incised and laid back to expose the cortical surface. Hemispheric wedge resections, as well as areal cortical removals, were accomplished by sucker aspiration combined with sharp instrument dissection. Transection of corpus callosum, anterior commissure, and massa intermedia was carried out following an earlier procedure most fully described in Myers and Henson.[5] The bone-flap afterwards was replaced and muscle and skin layers reapposed with surgical silk sutures. No antibiotics were used postoperatively. A minimum of 21 days of post-surgical recovery was allowed before functional testing was resumed.

Behavioral Test Procedures.—Visual guidance of paw or hand movement was tested in several ways.

A. Small morsels of food were attached to the end of a long rigid wire. This bait then was moved erratically in the different quadrants of the animal's visual fields at varying speeds and distances from the face. Normal animals pawed or reached rapidly and accurately in pursuit of the lure and generally seized it without fumbling.

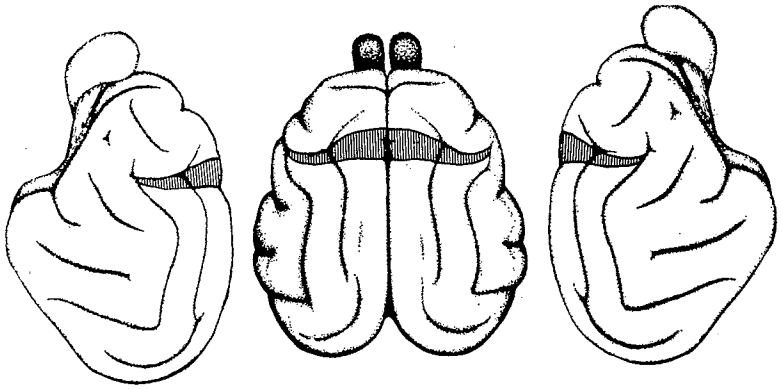

Fig. 1.—Schema of the bilateral wedge resections sustained by cat Dlt. The wedges, extending through the entire gray and white matter to the ventricular cavities, tended to disrupt direct connections between the occipital cortex and the sensory-motor cortex of the frontal pole.

B. Food morsels were placed at various points on a horizontal turntable of 3 ft. diameter that could be rotated at variable speeds. Normal animals, positioned next to the turntable, pawed or picked up the food objects as the objects approached or passed in rotation. Food morsels also were thrown to various loci on the stilled turntable to test accuracy of retrieve by the animal's paw or hand.

C. The ability of the animals to jump from one platform to another separated by various distances and at various heights was tested.

Anatomical Controls.—When postoperative testing was completed the animals were given a lethal dose of pentobarbital and perfused with 10% formalin. The extent of the cortical lesions and the completeness of the commissural sections was determined by detailed inspection and measurement both of the whole fixed brain and of gross brain slices. Where necessary, as in massa intermedia transections, extent of lesion was verified from microscopic study of sections stained after the techniques of Weil and Nissl. Descriptions of the lesions of individual animals follow in the text.

Results

Intrahemispheric Occipitocentral Linkages in Visuomotor Coordination.—Two cats and 2 monkeys were used to test the importance to eye-hand coordination of transgriseal and association-fiber conduction between the visual and the central motor cortical areas.

Cats: Cat Dlt sustained bilateral wedge resections as depicted in Figure 1. The wedges extended through the entire thickness of cortex and white matter of both hemispheres superiorly and entered the ventricular system across its entire roof. Laterally the wedges extended through both gray and white matter of gyrus suprasylvius anterior passing obliquely across the gyrus. Care was exercised that the interconnections between the frontal pole and the thalamus were not interrupted in the internal capsule and that blood supply to preserved structures was not disrupted.

Cat Dlt performed well all visuomotor tasks postoperatively. Her execution of these responses was, in fact, indistinguishable from that observed prior to the bilateral wedge resection. Deficiency was observed only on hindlimb tactile placing reactions bilaterally. The second cat, Snt, sustained com-

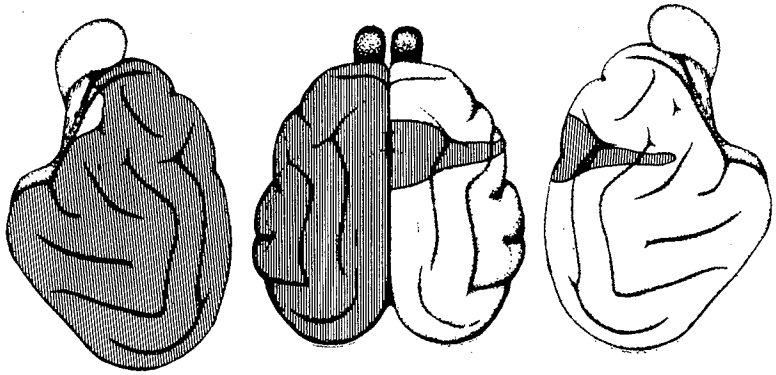

Fig. 2.—Schema of the lesions produced in cat Snt. The cortex was removed from the left hemisphere and the gray commissure of the thalamus divided at the first operation. The complete gray and white matter wedge of the right hemisphere was ablated at a second operation at a later time.

plete left neodecortication leaving only small fragments of gyrus frontalis and gyrus orbitalis as shown in Figure 2. Pyriform cortex and hippocampus remained undamaged. The interthalamic fibers of the intermediate mass were also divided in the midline at the same time.

This first operation on Snt resulted in the anticipated loss of visual responsiveness in the right visual half-field and deficiencies in placing, hopping, etc., of the right fore and hind legs. However, when tested 83 days after this operation centering and following of head and eyes to moving small objects in the left visual half-field continued apparently unimpaired. Snt struck accurately at small moving objects using the left paw. Using the right paw he struck only infrequently, and the movement when obtained was poorly directed and in most instances was ineffective. Snt was able to jump accurately between 2 platforms separated from each other as much as 33 inches.

At a second operation a wedge was resected from Snt's right hemisphere. The location and extent was similar to those wedge resections carried out bilaterally in cat Dlt, being, however, somewhat wider in rostrocaudal direction and extending more laterally to involve the superior two-thirds of gyrus ectosylvius anterior, including both its gray and white matter.

When tested 30 days later there were no apparent abnormalities in visuomotor function beyond those observed following the first operation. Snt continued to center and to follow with the eyes and head small objects moved irregularly through the left visual field. Using the left paw he struck at and retrieved with seemingly undiminished accuracy meat fragments moved or dropped within his left visual field. The deficiencies of the right visual field remained unaltered.

Monkeys: Monkey 542 sustained bilateral posterior parietal wedge resection as depicted in Figure 3. Superiorly, the resection extended through the entire depth of the gray and white matter bilaterally, entering the ventricles along their entire mediolateral extent as they overlay the thalamus. Laterally, each lesion interrupted the centrum semiovale widely as it lay superior and lateral to the thalamus, internal capsule, and putamen. Still more laterally the lesion joined the sylvian fissure. In this manner continuity between the frontoparietal and the occipitotemporal sectors of the hemispheres was restricted to a narrow isthmus consisting essentially of the mass of the thalamus and basal ganglia and of the gray and white matter of the insula (Fig. 4).

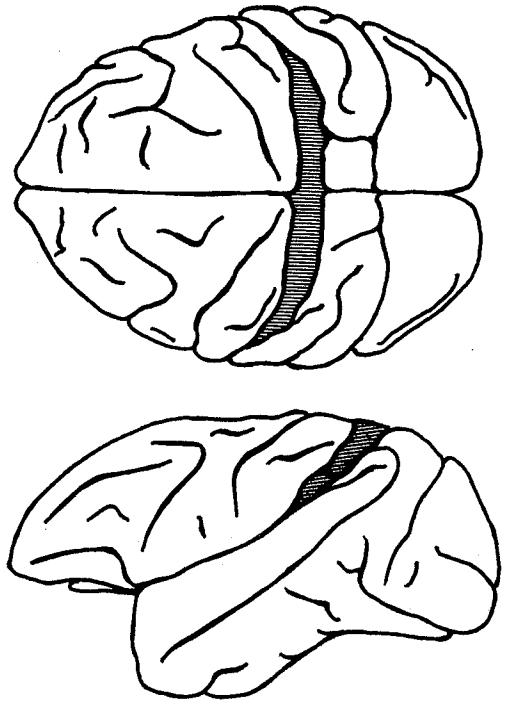

Fig. 3.—Schema of the bilateral wedge removal sustained by Monkey 542. This interruption of the gray and white matter extended through the posterior parietal region and completely split the hemispheres transversely except for the thalamus and the region of the insula buried in the sylvian fissure.

When repeatedly tested from 21 days to 1 year after the lesions Monkey 542 performed all visuomotor tasks without detectable deficit. His pursuit and prehension of fruit, peanuts, or raisins passed irregularly before him or tossed at random on the rotating turntable remained closely coordinated with their displacement through his visual space. Use of his hands and feet in climbing about the cages, jumping, and generally responding also remained unimpaired.

Fig. 4. — Weil-stained microscopic section through the isthmus created by the bilateral transverse wedge removals in Monkey 542. Note there remained only the mass of the thalamus and the basal ganglia together with the gray and white matter of the insula to conduct impulses between the hind and fore sectors of the hemispheres. The internal capsule lay between the thalamus and the corpus striatum and remained undamaged. The gyrus overhanging the insula on the right belonged to the parietal operculum. Just caudal to the above section this gyrus was found to be completely separated from the occipitotemporal sector of the hemisphere by the wedge resection.

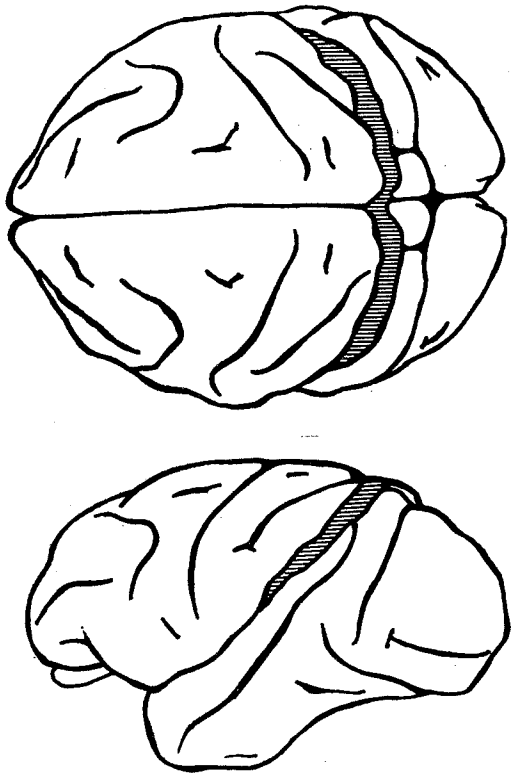

Fig. 5.—Bilateral transverse wedge resection produced in monkey 12. Again, the resections interrupted the entire thickness of gray and white matter of the parietal lobes extending into the ventricular system across the width of its roof on the 2 sides. In this animal the interruptions were more posteriorly placed leaving very little of the posterior parietal region attached to the occipitotemporal sector and preserving a greater extent of the anterior parietal lobe as part of the frontoparietal sector. In addition, the resections were carried forward obliquely across the surface of the insulae of the 2 sides through the sylvian fissures.

Monkey 12 sustained bilateral wedge resections similar to those of Monkey 542, resections being, however, more posteriorly located in the parietal lobes (see Fig. 5). In addition, the resections were extended to include the gray and white matters of the insulae of the 2 sides including interruption of the external and extreme capsules, the uncinate fasciculi, and the claustra as may be seen from Figure 6.

This monkey, like 542, failed to exhibit definite postoperative deficiencies in eye-hand control on any of the tests described. Also like 542, this monkey was indistinguishable from normal animals on casual observation in the cage situation.

Interhemispheric Linkage in Crossed Visuomotor Coordination.—Five cats and 3 monkeys were selected to test the importance of the forebrain commissures to crossed eye-hand coordination. The sensorimotor cortex of the right hemisphere and the visual cortex of the left hemisphere were removed in all these subjects. Type lesions for the cats and for the monkeys are illustrated in Figures 7 and 8. These animals afterwards exhibited the expected paretic symptoms and loss of placing reactions of the members of the left half of the body and a lack of responsiveness in the right visual half-field. Through the whole series of tests there was no definite indication of difficulty in the discrete use of the right hand or paw in the pursuit and

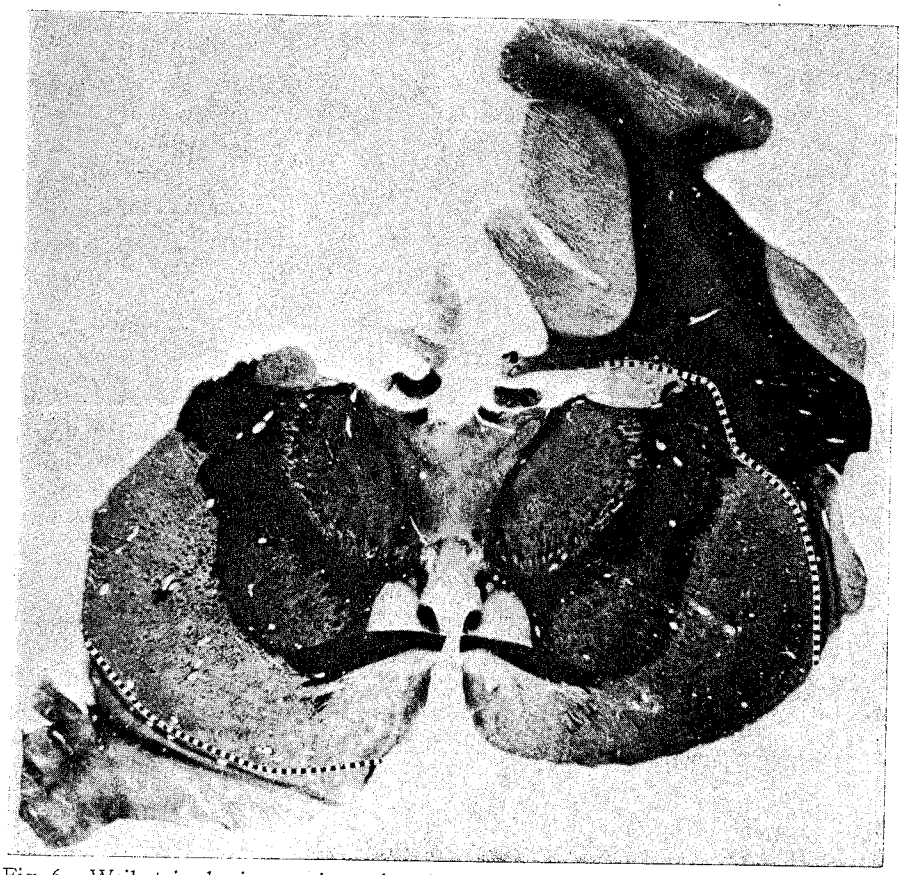

Fig. 6.—Weil-stained microscopic section through the isthmus created by the bilateral transverse wedge removals in Monkey 12. Because of differences in the tilts of the lesions of the 2 sides it was impossible to clearly portray the extent of the lesions on the 2 sides in one section. Study of serial sections, however, indicated that the interruption of the gray and white matter of the parietal lobes of the 2 sides was complete as was that of the gray and white matter of the insulae bilaterally. The verified extent of the lesion is indicated by the dashed lines. Note that the only available interconnections remaining between the 2 sectors of the brain were through internuncials of the thalamus and corpus striatum including innominate substance.

prehension of small objects presented in the left visual half-field. However, awkwardness in balance and poise of the body was seen in the monkeys due presumably to the combination of left hemiparesis and the imposed necessity of reaching rapidly with the functional right hand past the midplane into the left visual space. Visual placing reactions were well preserved as tested through the functional right forelimb.

The corpus callosum and anterior commissure were next completely transected in these animals. After a minimum of 21 days of postoperative recovery, both the cats and the monkeys were again subjected to the complete series of tests. No sign of further deficiency was observed in the visual control of right limb responses. Using this limb the animals were able to paw or grab with accuracy small morsels of food dangled or irregularly passed through the left half-field of vision. They easily clawed or plucked food particles tossed in various places before them. They centered and followed with their eyes and head small objects as they were presented. Further, despite the forebrain commissurotomy, they continued to perform quite well the crossed visual placing reactions.

Comment

Bilateral wedge resections interrupting direct gray and white matter conduction be-

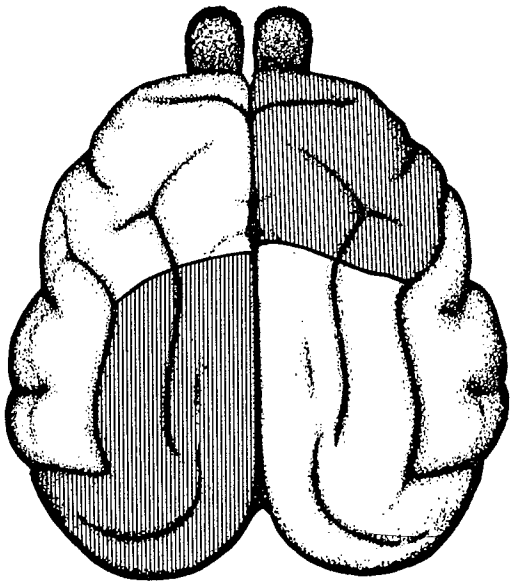

Fig. 7.—The type of lesion made in the series of 5 cats in which the right sensorimotor and the left occipital cortex was removed at 1 operation. Afterwards the animals exhibited well-coordinated crossed eye-hand coordination in which they could accurately swat meat fragments dangled in their left visual half-field with their right paws.

tween the occipitotemporal and the frontoparietal sectors of the hemispheres have failed to interfere with the visual control of limb movement in either the cat or the monkey. These findings accord well with the clinical observations of Penfield [6] who failed to find interference with volitional movements in humans after incomplete interruptions of associational connections to the precentral gyrus. Transgriseal and arcuate fiber conduction between the occipitotemporal and the central motor regions seem not to be essential to the visual coordination of hand movements.

Section of the corpus callosum and anterior commissure in animals with the occipital centers of one hemisphere and the pre- and postcentral motor centers of the other destroyed did not block the surviving crossed eye-hand coordination. It may be concluded that visual inflow into the preserved occipital lobe still may effectively direct movements of the limb controlled through the central convolutions of the opposite hemisphere in the absence of commissural linkages of a forebrain type. A conclusion similar to this may be drawn from Akelaitis's [1] observation that corpus callosum sectioned humans retain the capacity to accurately track with either hand objects presented in either visual half-field. Downer's [3] description of an apparently complete failure of crossed eye-hand coordination in monkeys with midsagittal section of optic chiasma and corpus callosum remains at variance with these findings.

With all possible transgriseal or corticocortical connections between visual and motor areas surgically eliminated, how may the visual cortex continue to extend its hegemony over the motor reaction system? This question remains unanswered. Conceivably, as suggested by Penfield,[7] the information from visual cortical regions necessary for guidance of response may reach precentral cortex after relay through brainstem centers, thereby circumventing need for the pathways destroyed in the present study. Alternative-

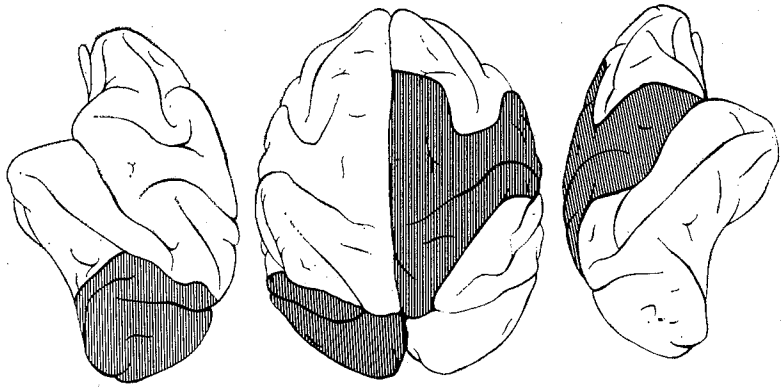

Fig. 8.—Crossed lesions carried out in 3 monkeys. The entire occipital lobe was amputated from the left hemisphere and the entire pre- and postcentral gyri removed from the right hemisphere. Though the monkeys were clumsy in ambulation due to left hemiplegia, they still retained an excellent ability to snatch discrete objects passed through their left visual field using their right hand.

ly, the precentral convolution may not be in any direct sense involved in the mediation of the visual guidance of motor response, but, instead, may serve merely a background servomechanical and facilitatory function setting the scene for a motor response initiated and directed from elsewhere, as has been contended by Lashley.[4] In this latter instance visual guidance may be accounted for fully by corticofugal influences from visual areas projecting directly onto motor mechanisms organized at brainstem levels. Further insight into these relationships must await future investigation.

Summary

Elimination of gray and white matter conduction between the occipital visual cortex and the central motor cortex failed to interrupt the visual guidance of limb movement in cats and monkeys. Further, complete transection of the forebrain commissures failed to halt eye-hand coordination of a cross-hemisphere type. It was concluded that if visual cortical impulses require routing to central motor cortex for the visual control of limb movement, such routing may be successfully transmitted through brainstem centers. The alternative suggestion was made that visual control of limb movements may be brought about by transmission of visual impulses from occipital cortex directly onto motor mechanisms in the brainstem and spinal cord without need for channeling through motor cortex.

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